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Behavioral Development: Timing is Everything

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Behavioral Development: Timing is everything

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Summary

Paedomorphism can be a mechanism for differentiation between species. Here the authors demonstrate that bonobos take longer to reach adult levels of two behaviors than do chimpanzees, providing an empirical demonstration of this hypothesis among our closest relatives.

One challenge in evolutionary biology is explaining how relatively large changes between species can arise in a relatively short period of time. A potential mechanism for this change is heterochrony, in which development speeds up, slows down, or is truncated in one species relative to another [1]. The resulting effects on morphology and behavior can be dramatic.

A well-known example of heterochrony exists among a group of foxes in Russia involved in a decades-long study of domestication [2]. Juvenilization is a hallmark of domesticated species [3, 4], and geneticist Dmitry Belayev hypothesized that selection for a single behavior, tameness, could cause the plethora of changes seen during the process of domestication due to effects on developmental processes. Belayev chose a single criterion (willingness to interact with humans) to determine which foxes bred each generation. Within a few generations, the foxes were not only domesticated, but had developed characteristics typical of juveniles, such as the piebald coats and large, floppy ears.

Heterochrony also exists outside of domestication. It has been proposed that some of the differences between bonobos and chimpanzees (and, in fact, humans and other apes [5]), can be explained by paedomorphism. Bonobos, in comparison to chimpanzees, show paedomorphism in anatomy [6, 7] as well as some juvenilized behaviors [8-10]. Although this indicates that their behavior may also be paedomorphic with respect to chimpanzees, no study has been done to explicitly investigate this. In the current paper, Wobber and colleagues investigate whether the marked behavioral differences seen between chimpanzees and bonobos, the congeneric apes most closely related to humans, might be a result of changes in development speed [11]. Specifically, they investigate paedomorphism; whether changes in behavior may be due to slower - or the early curtailment of - development in one species as compared to the other.

In the initial study, the authors examined food sharing frequency in both apes. Apes were simultaneously given access to a food resource, which they could either monopolize or share. Tolerance around food is uncommon in adult primates [12], so willingness to share in adulthood may be a sign of juvenilization. Adult bonobos were more likely to share than were adult chimpanzees. Moreover, bonobos showed no change in tolerance as they aged; juveniles were just as likely as adults to share food. Chimpanzees, on the other hand, were as tolerant as bonobos when they were younger, but became much less tolerant by adulthood. In other words, the two ape species started out with similar levels of tolerance, however while bonobos maintained their tolerance, chimpanzees became less so. Thus in comparison with the chimpanzees' behavior, bonobos' behavioral development is paedomorphic.

The authors next examined whether bonobos' ability to inhibit was altered with respect to chimpanzees in another food situation. The authors first designed an inhibition task that could be used with juveniles. In an initial test, the apes had to choose from among three experimenters, only two of which had food. If they requested food from the middle experimenter, who did not have food, the trial was over. Thus, the apes had to inhibit their tendency to ask each experimenter in turn, and instead skip over the middle individual, to get all of the food. The chimpanzees were very successful at this task at all stages of development. Older bonobos were equally adept as older chimpanzees. However, the younger bonobos were less capable than either the older bonobos or the chimpanzees. Thus, while bonobos and chimpanzees reached the same level of competence, the bonobos did so at an older age, indicating retarded development as compared to the chimpanzees.

To follow up, the authors utilized a slightly more demanding inhibition task, a reversal learning paradigm, with an older group of apes. This allowed them to test whether there were differences in inhibitory skill which lingered in to adulthood. The apes were initially exposed to one experimenter who had food and one who did not. After their preferences were established, the experimenters switched roles, so the apes had to switch their preferences to get the food. Again, adult apes of both species reached similar levels of competence at this task, although chimpanzee adults were also slightly, but not significantly, better in the first trials of the session than the bonobos. Once again, the bonobos became adept at the task at a later age than did the chimpanzees. Taken together, these results indicate that bonobos' behavior is paedomorphic with respect to chimpanzees. They are more likely to retain juvenile traits (tolerance) in to adulthood and develop other cognitive skills (inhibition) at an older age than do chimpanzees.

Of course, when studying something as complex as the development of an organism, one of the challenges is to avoid oversimplification. Heterochrony can result from a variety of different mechanisms [1], and as with any evolutionary theory it is important to avoid just-so stories which aren't empirically validated [13]. One example of a research area in which popular belief may outstrip scientific evidence is the case of the domestic dog. Although it is commonly assumed that, as a result of domestication, dogs are paedomorphic in comparison to wolves, the evidence is actually mixed [14, 15]. One commonly cited example of paedomorphism in dogs, the truncated snout, is also correlated to better vision. Thus, this trait may have been selected for due to its benefits to the dogs, rather than being the byproduct of domestication ([16, 17]; although see [18] for a developmental perspective). While this may seem like splitting hairs, if the goal is to understand evolutionary scenarios, it is actually quite important; if paedomorphism doesn't explain the evolution of some behavior, then we must seek out the mechanism which does [1].

The same holds true for our own evolution. In our quest to figure out what it is that sets humans apart from other apes, a common perception has developed that humans are paedomorphic. We appear to be extremely juvenilized as compared to the other apes, and arguments that we, too, are paedomorphic have been forwarded for at least a century [5, 19]. However, this approach ignores other evidence which indicates the opposite, or peramorhposis. In particular, the argument has been made that our brain is overdeveloped, with additional synaptic complexity, rather than the result of plasticity due to juvenilization [1]. If we are to understand our own evolution, it is critical that we approach the evidence carefully.

One of the benefits of studies such as this one [11] is that the heterochrony hypothesis is empirically validated. The authors demonstrate not only that adult chimpanzees and bonobos behave differently, but also that the developmental trajectory differs between the two species. Although future studies will undoubtedly complicate the picture, they would do well to take similar care in gathering the evidence. In this way, we may eventually tease apart which factors led bonobos and, by extension, other species, to be selected for altered developmental speeds, and understand how this affected their evolution.

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Figure Caption: Two adult female chimpanzees look on as another eats a frozen fruit juice treat. Although chimpanzees are generally tolerant of each other's presence, they share much less food as adults than as juveniles. On the other hand, bonobos share as much as adults as they did as juveniles, indicating different developmental trajectories between the species. This is evidence for behavioral paedomorphism in bonobos. Photograph by Sarah F. Brosnan, taken at the Keeling Center of MD Anderson Cancer Center.